BIRD COMMUNITIES IN THINNED VERSUS UNTHINNED SIERRAN MIXED CONIFER STANDS

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ABSTRACT.—We used point counts and nest monitoring to compare avian community composition and nesting success in thinned and unthinned stands of commercially managed Sierran mixed conifer forest. We conducted point counts and monitored 537 active nests of 37 species on 10 study plots during three consecutive breeding seasons in the northern Sierra Nevada. All 10 study plots had experienced a similar long term management history that included fire suppression and single-tree selection logging, but five of the plots also underwent a protocol of combined commercial and biomass thinning 5–8 years prior to the beginning of the study. Pooling species by nest substrate, we found that detections of ground-nesting bird species were similar on thinned and unthinned plots, but we detected canopy-, cavity-, and especially shrub-nesting species much more frequently on the thinned plots. Nest success rates were not statistically different between thinned and unthinned plots for ground-, shrub-, canopy-, or cavity-nesting species. Thinned stands were characterized by significantly less canopy cover, significantly lower density of small and medium conifers, and significantly greater understory cover and deer brush (*Ceanothus integerrimus*) cover than the unthinned stands. We surmise that the thinning protocol stimulated vigorous shrub growth, and conclude that forest conditions associated with a relatively open canopy and a well-developed shrub understory are highly beneficial to numerous breeding bird species in the Sierran mixed conifer community, including many species that may not nest or forage in the understory. Forest thinning that promotes vigorous shrub growth may correlate with an increased abundance of nesting birds, at least within stands affected by historical fire suppression and single-tree selection logging. *Received 1 October 2002, accepted 5 March 2003.*

Logging practices and human-altered fire regimes have changed forest structure and composition across much of the Sierra Nevada since the mid-Nineteenth Century (Franklin and Fites-Kaufmann 1996, Gruell 2001). Timber harvest practices and fire suppression throughout much of the region generally have reduced the frequency of low intensity fires, reduced the number of large trees, increased the density of smaller trees, and possibly reduced the extent of shrub cover (Weaver 1974, Vankat and Major 1978, McKelvey and Johnston 1992, Chang 1996). Concomitantly, forest composition has shifted substantially as altered fire regimes have favored the recruitment of shade tolerant tree species such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) at the expense of less shade tolerant pines (Agee et al. 1978, Bonnickson and Stone 1983, Weatherspoon et al. 1992, Chang 1996). These changes in forest structure and composition may have had far-reaching effects on avian community composition (Beedy 1982, Raphael et al. 1987, Hejl

1994), but adequate data for inferring historical avian community structure are lacking.

Across much of the Sierra Nevada, fuel loads resulting from decades of fire suppression have complicated the use of prescribed fire. If forest thinning can mimic at least some aspects of fire-induced ecological processes and forest structure, it may be an important tool for promoting wildlife species associated with the forest attributes that fire suppression discourages, especially in areas where land managers are reluctant to use prescribed fire. However, relatively little is known about the potential for silvicultural treatments to mimic the ecological functions of fire (Centers for Water and Wildland Resources 1996). Thinning protocols in Pacific Northwest second-growth forests have been shown to increase the abundance of breeding birds (Hagar et al. 1996) and other wildlife species (Sullivan et al. 2001) by promoting a more complex vertical stand structure. The limited information available from Sierran ecosystems, however, is inadequate for assessing whether biomass thinning—the removal of small-diameter, low value trees from dense stands—may effectively spur vigorous shrub growth, and thereby benefit shrub-associated bird species. While Sierran mixed conifer forest stands with rel-

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atively open canopies and well-developed shrub understories host higher densities of birds than stands with high canopy closure and poorly developed shrub understories (Beedy 1981), it remains to be established that biomass thinning can effectively produce these conditions, and if it can, that birds respond favorably.

Biomass thinning has been a common treatment on Sierran timberlands since the 1978 passage of the Public Utility Regulatory Policies Act, which created a market for the power generated by burning chipped trees (T. E. Kucera and R. H. Barrett unpubl. data). Biomass thinning has been implemented extensively across northern California's forests, with an estimated 24,000 ha of California forest thinned annually during the mid-1990s (T. E. Kucera and R. H. Barrett unpubl. data). In addition to generating extra income when energy market conditions are favorable, biomass thinning also may reduce the risk of fire reaching the forest canopy, may lower the competition among remaining trees for light, soil moisture and nutrients, and may increase the value of the wood products that ultimately can be harvested from the remaining trees (Helms and Tappeiner 1996, T. E. Kucera and R. H. Barrett unpubl. data). To the extent that the technique yields forest stands with relatively open canopies and well-developed shrub understories, it may increase the density of nesting birds, especially shrub-nesting species. Alternately, if the removal of small-diameter understory trees fails to stimulate vigorous shrub growth, it may have little effect, or even a negative effect, on shrub-associated bird species.

We compared breeding bird communities of thinned and unthinned stands of commercially managed, Sierran mixed conifer forest (Mayer and Laudenslayer 1988), where the historical management legacy included fire suppression and repeated stand entries for single-tree selection logging. We sought to ascertain how forest characteristics induced by combined commercial and biomass thinning correlate with avian community composition and nesting success in stands that had undergone these widely implemented management practices. We further sought to identify one or more simple, easily quantified habitat attributes associated with high densities of nesting birds or

high levels of nest success. Such attributes could guide Sierra Nevada land managers interested in incorporating the habitat needs of breeding birds into their forest management plans.

STUDY AREA AND METHODS

Study area.—We worked on Sierra Pacific Industries timberlands in Tehama County, California, on the western slope of the Sierra Nevada. Our 10 study plots were dominated by Sierran mixed conifer forest, comprised of varying proportions of white fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), incense cedar, and sugar pine (*P. lambertiana*), with occasional small stands and single individuals of California black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepis*), as well as mountain dogwood (*Cornus nuttallii*), bigleaf maple (*Acer macrophyllum*) and California hazelnut (*Corylus cornuta*). Deer brush (*Ceanothus integerrimus*) was the dominant understory shrub, but other common shrubs included mahala mat (*C. prostratus*), creeping snowberry (*Symphoricarpos acutus*), Sierra gooseberry (*Ribes roezlii*), and to a lesser extent, greenleaf manzanita (*Arctostaphylos patula*), poison-oak (*Rhus diversiloba*), and Sierra chinquapin (*Castanopsis sempervirens*). All 10 plots were primarily south facing, with mean slopes ranging from 5–15°.

Study design and sampling.—During the spring of 1998 we identified two patches of forest on nearby, roughly parallel south-facing slopes that were similar in aspect, slope, forest type, and seral stage, but differed in that a protocol involving both biomass thinning and commercial thinning (single tree selection) was applied to one of them between 1990 and 1993 (different portions of the slope were thinned during different years). The thinning treatment involved removing some individually selected merchantable trees (commercial thinning) as well as smaller trees and saplings (biomass thinning) to retain vigorous, healthy trees spaced approximately 8.2 m apart (S. Self pers. comm.). Both patches had undergone similar histories of previous silviculture treatments. The patch that was thinned during the early 1990s underwent selection overstory logging during the late 1930s and early 1940s, again between 1978 and 1988, and once more

in a small area during 1994. The unthinned patch, about 5 km to the northwest, underwent similar overstory logging during the late 1950s and again during 1978 and 1994.

We established five 36-ha study plots in each patch by randomly selecting starting points on maps of the two areas of interest, and then extending boundaries out in random cardinal directions. Boundaries were turned 90° when they approached within 200 m of another plot, or within 100 m of a riparian buffer area that had been managed differently than the upland forest. The resulting thinned plots (centered on 40° 07′ N, 121° 34′ W) were located at 1,250–1,430 m elevation, similar to the unthinned plots (centered on 40° 11′ N, 121° 35′ W), which were located at 1,160–1,550 m elevation. We stress that historical overstory logging occurred previously on both sets of plots, so our unthinned plots were unthinned only in the sense that they did not undergo the 1990s biomass and commercial thinning treatment.

To ensure that we devoted equal effort to nest searching on thinned and unthinned plots and avoided bias from uneven observer abilities, field crews alternated days searching for nests on the thinned plots and unthinned plots. We searched for nests according to the guidelines in Martin and Geupel (1993), and recorded nest observations and habitat data in accordance with standard nest-monitoring guidelines described in Martin et al. (1997). Once we discovered an active nest, we visited it at least once every four days, but usually every two days. We considered nests successful if they fledged at least one young bird. We based nest fate determinations on nesting intervals described in Ehrlich et al. (1988), and the criteria described in Manolis et al. (2000), which provide standardized guidelines for determining whether nests succeeded, and for incorporating nests with uncertain fates into analyses.

We conducted point counts three times in each of three years (1998–2000) between 23 May and 18 June at nine points (hereafter a transect) on each study plot. Nine points, the maximum number that we could fit on each plot while still ensuring that points were spaced 200 m apart, were arrayed in a regular grid and were ≥100 m from the plot boundary. Each year three observers trained in bird

identification conducted all the point count surveys, such that each replicate was conducted by a different observer, and all 10 plots were surveyed by the same three observers. Point counts began within 10 min of official local sunrise and generally were completed by 09:00. The order of points was shifted for each repeated survey so that each point was surveyed once each year during the early, middle, and later part of the morning. Point counts were not conducted on mornings with rain or enough wind to generate substantial noise interference. Each point count lasted 5 min, during which observers noted every bird seen or heard, and recorded birds detected within a 50-m radius separately from birds detected beyond 50 m. Only birds detected within the 50 m radius were included in the analysis of bird communities. When observers detected individual birds they believed had been detected from a previous point on the same day (generally very loud species that could be heard calling from the same area at two consecutive point count stations), they noted them as such, and we included only the first detection in our analysis.

While we support recent calls for researchers to utilize distance sampling or some other means of correcting point count data for detectability (Rosenstock et al. 2002, Williams et al. 2002), we believe our use of a 50-m detection radius was sufficient to safeguard against spurious results. In another study of unthinned Sierran forest involving many of the same species present on our plots, De-Sante (1986) determined that basal detection radii (distance band from the observer within which distance from the observer to a bird is unrelated to detection probability) for most species well exceeded 50 m. Nevertheless, to test for potentially confounding variation in the detection function between our two sets of plots, we used a 2×2 contingency table to compare the ratio of the number of birds detected within 50 m of the observer to the number of birds detected beyond 50 m from the observer on thinned and unthinned plots (Buckland et al. 2001). If detectability was greater on the thinned plots compared to the unthinned plots, we would expect that the proportion of all detections that were beyond 50 m of the observer would be greater on the thinned plots than on the unthinned plots. We

TABLE 1. The five thinned Sierra forest plots exhibited less canopy cover, lower density of small and medium conifers, and greater deer brush cover and overall understory cover than the five unthinned plots. Other habitat variables we examined were similar across both plot types. Values are mean ± SD. Data are from northern California, 1998–2000.

Habitat variable	Thinned plots	Unthinned plots	t	P
Canopy cover (%)	53.0 ± 7.0	66.3 ± 7.4	2.6	0.032
Canopy height (m)	23.3 ± 1.5	21.4 ± 2.5	1.3	0.233
Understory cover (%)	27.2 ± 7.0	17.6 ± 2.2	2.7	0.029
Deer brush cover (%)	15.4 ± 3.4	4.7 ± 3.0	4.8	0.001
Oak density (trees/ha)	12.5 ± 15.4	22.3 ± 18.4	0.8	0.437
Large conifer density (trees/ha)	74.2 ± 9.0	77.7 ± 13.6	0.4	0.683
Medium conifer density (trees/ha)	91.4 ± 33.8	182.0 ± 24.0	4.4	0.002
Small conifer density (trees/ha)	97.4 ± 70.8	329.7 ± 124.0	3.3	0.012
Snag density (trees/ha)	15.8 ± 14.4	19.7 ± 3.6	0.5	0.614

know of no previously published studies examining the effects of forest thinning on bird detectability.

We collected habitat data between 1998 and 2000 in accordance with the guidelines provided by Martin et al. (1997). This involved assessing vegetation structure and composition within 5.0-m radius subplots (for shrubs, saplings, and ground cover) and 11.3-m radius subplots (for trees and snags) at 36 points (12 each year) in a systematic array covering each of the 10 study plots. Within each vegetation subplot, we measured canopy cover with a spherical densiometer, measured canopy height with a clinometer, counted the number of small (<23 cm dbh), medium (23–38 cm dbh) and large (>38 cm dbh) conifers, counted the number of oaks and the number of snags (≥2 m tall), and visually estimated the percent cover provided by deer brush (the most abundant shrub species on the study plots), and the percent cover provided by all woody plants <5 m tall (hereafter the understory component of the forest). Although Block et al. (1987) showed that visual cover estimates can vary substantially among observers, our sampling design insured that each observer sampled an equal number of subplots on both the thinned plots and the unthinned plots. We considered trees <5 m tall or <8 cm dbh to be saplings, and did not include them in tree density estimates, although they did contribute to the understory percent cover. For each habitat variable, we averaged values from the 36 subplots to produce a single plot-wide mean for each of the 10 study plots.

Data analysis.—In accordance with recent guidelines proposed by Manolis et al. (2000), our calculation of nest success rates incorporates nests with uncertain fates, with exposure terminated on the last observed active date. We assumed nests with known fates terminated at the midpoint between the last observed active date and the first observed inactive date (Manolis et al. 2000).

We pooled nest success data across species within each of four groups of birds: ground-nesting, shrub-nesting, canopy-nesting, and cavity-nesting species. For each group we calculated daily nest success rates on the thinned plots and the unthinned plots, using the methods of Mayfield (1961, 1975). We used t-tests to compare point count detections of each group on thinned and unthinned plots, and to compare habitat attributes of thinned and unthinned plots. We used χ^2 tests with Yates correction for continuity to assess whether the numbers of nests of each species or group of species on thinned versus unthinned plots differed from the expected 1:1 ratio. The significance threshold for all statistical tests was $P < 0.05$, and all tests were two tailed. We used SYSTAT (SPSS, Inc. 1997) to perform all statistical tests.

RESULTS

General plot characteristics.—Compared to unthinned plots, thinned plots exhibited significantly lower canopy cover, medium conifer density, and small conifer density, and significantly higher understory cover and deer brush cover (Table 1). Among the nine habitat variables we examined, deer brush cover differed most strongly between the two sets of

plots (Table 1). Understory cover was negatively correlated with canopy cover ($r^2 = 0.42$, $P = 0.044$), as was deer brush cover ($r^2 = 0.63$, $P = 0.006$). Canopy height, oak density, large conifer density, and snag density were statistically equivalent on the two sets of plots (Table 1).

Point counts.—During nine point count transects (three replicates during each of three years), we recorded 44 bird species on the thinned plots, 39 of which also were recorded on the unthinned plots; no bird species were detected on the unthinned plots only. Of those 44 species, significantly more of them (32) were detected more frequently on the thinned plots than on the unthinned plots ($\chi^2 = 8.2$, df $= 1$, $P = 0.003$).

Excluding species whose nests we never found on any of the 10 study plots, we detected a mean of 48.6 individual birds per transect on the thinned plots compared to 31.0 birds per transect on the unthinned plots ($t = 7.08$, df $= 8$, $P = 0.0001$; Table 2). Thinned plot and unthinned plot detection totals of ground-nesting species were not statistically different ($t = 0.09$, df $= 8$, $P = 0.93$; Table 2), but thinned plot totals were much higher than unthinned plot totals for pooled shrub-nesting species ($t = 3.69$, df $= 8$, $P = 0.006$; Table 2), pooled canopy-nesting species ($t = 4.61$, df $= 8$, $P = 0.002$; Table 2), and pooled cavity-nesting species ($t = 3.80$, df $= 8$, $P = 0.005$; Table 2).

Pooling all species, we recorded 51.1% of bird detections beyond 50 m of the observer on the thinned plots, compared to 58.6% on the unthinned plots ($\chi^2 = 58.9$, df $= 1$, $P < 0.0001$).

Nest monitoring.—The number of active nests we found on individual study plots correlated significantly with the mean number of point count detections of species we found nesting on at least one of the 10 study plots ($r^2 = 0.85$, $P = 0.0002$). We found 537 active nests on the 10 study plots; 139 (26%) were located on the unthinned plots, and 398 (74%) were located on the thinned plots (Table 3). Nest totals on the thinned plots were significantly higher than on the unthinned plots for ground-nesting species ($\chi^2 = 14.1$, df $= 1$, $P = 0.0004$), shrub-nesting species ($\chi^2 = 86.4$, df $= 1$, $P < 0.0001$), canopy-nesting species ($\chi^2 = 10.9$, df $= 1$, $P = 0.0007$), and cavity-

nesting species ($\chi^2 = 27.5$, df $= 1$, $P < 0.0001$; Fig. 1a), as well as for all species pooled ($\chi^2 = 124.0$, df $= 1$, $P < 0.0001$).

We determined the fate of 470 of the 537 active nests we observed (Table 3). We observed significantly more successful nests of shrub-nesting species ($\chi^2 = 35.8$, df $= 1$, $P < 0.0001$), canopy-nesting species ($\chi^2 = 5.78$, df $= 1$, $P = 0.011$), and cavity-nesting species ($\chi^2 = 8.49$, df $= 1$, $P = 0.002$) on the thinned plots (Fig. 1b). Although we found nearly twice as many ground nests on the thinned plots as compared to the unthinned plots (Fig. 1a), the difference in numbers of successful nests was not statistically significant ($\chi^2 = 3.45$, df $= 1$, $P = 0.067$). We observed successful nests of four individual species in significantly greater numbers on the thinned plots than on the unthinned plots: Dark-eyed Junco (*Junco hyemalis*; $\chi^2 = 4.36$, df $= 1$, $P = 0.024$), Dusky Flycatcher (*Empidonax oberholseri*; $\chi^2 = 21.0$, df $= 1$, $P < 0.0001$), Hammond's Flycatcher (*Empidonax hammondii*; $\chi^2 = 8.10$, df $= 1$, $P = 0.002$), and Black-headed Grosbeak (*Pheucticus melanocephalus*; $\chi^2 = 7.11$, df $= 1$, $P = 0.004$). We observed no species with significantly more successful nests on the unthinned plots.

On both the thinned and the unthinned plots, cavity-nesters had relatively high daily nest success, shrub and canopy nesters had intermediate nest success rates, and ground-nesters had the lowest nest success rates (Fig. 1c). There was a nonsignificant tendency for ground, canopy, and cavity nests on unthinned plots to succeed at greater rates than those on thinned plots, but differences in daily nest success rates were not statistically different between thinned and unthinned plots for any of the four groups of species (Fig. 1c).

DISCUSSION

Our finding that a significantly greater proportion of birds were detected beyond 50 m of the observer on the unthinned plots than on the thinned plots does not support the hypothesis that detectability was greater on the thinned plots. The great majority of point count detections in forested habitat are generally auditory, rather than visual, and the proportion of auditory detections increases with distance from observer. The increased shrub cover on the thinned plots may have reduced

TABLE 2.   We detected most shrub-, canopy- and cavity-nesting species much more frequently on thinned plots than on un-thinned plots, while ground-nesting species were recorded at relatively similar frequencies on the two sets of plots. Detections per transect indicates the mean number of birds detected within a 50-m radius during nine replicates (three replicates during each breeding season) of each point count transect. Each point count transect comprised nine point counts. Results are presented for species with at least one nest found on any of the study plots. Values are mean ± SD. Data are from northern California, 1998–2000.

Species	Detections per transect	
	Unthinned plots	Thinned plots
Ground-nesting species		
Mountain Quail (*Oreortyx pictus*)	0.20 ± 0.22	0.13 ± 0.13
Townsend's Solitaire (*Myadestes townsendi*)	0.38 ± 0.17	0.15 ± 0.05
Nashville Warbler (*Vermivora ruficapilla*)	2.42 ± 0.99	0.82 ± 0.77
Spotted Towhee (*Pipilo maculatus*)	1.40 ± 0.63	1.38 ± 0.54
Dark-eyed Junco (*Junco hyemalis*)	3.82 ± 0.97	5.02 ± 0.62
Fox Sparrow (*Passerella iliaca*)	0.35 ± 0.19	1.16 ± 0.92
Pooled	8.57 ± 1.63	8.66 ± 1.25
Shrub-nesting species		
Dusky Flycatcher (*Empidonax oberholseri*)	0.07 ± 0.09	5.98 ± 1.92
Hermit Thrush (*Catharus guttatus*)	0.13 ± 0.16	0.36 ± 0.36
Cassin's Vireo (*Vireo cassinii*)	1.49 ± 0.42	3.04 ± 0.67
Yellow Warbler (*Dendroica petechia*)	0.11 ± 0.10	0.46 ± 0.44
MacGillivray's Warbler (*Oporornis tolmiei*)	0.11 ± 0.07	0.29 ± 0.13
Black-headed Grosbeak (*Pheucticus melanocephalus*)	1.58 ± 0.57	1.16 ± 0.52
Lazuli Bunting (*Passerina amoena*)	1.86 ± 0.45	1.13 ± 0.59
Chipping Sparrow (*Spizella passerina*)	0.24 ± 0.04	0.80 ± 0.36
Pooled	5.59 ± 0.66	13.22 ± 4.08
Canopy-nesting species		
Anna's Hummingbird (*Calypte anna*)	0.02 ± 0.04	0.27 ± 0.42
Calliope Hummingbird (*Stellula calliope*)	0.00 ± 0.00	0.04 ± 0.09
Western Wood-Pewee (*Contopus sordidulus*)	0.07 ± 0.09	0.18 ± 0.15
Hammond's Flycatcher (*Empidonax hammondii*)	0.11 ± 0.12	2.58 ± 0.18
Steller's Jay (*Cyanocitta stelleri*)	1.42 ± 0.69	0.53 ± 0.28
American Robin (*Turdus migratorius*)	0.22 ± 0.27	0.49 ± 0.18
Warbling Vireo (*Vireo gilvus*)	0.13 ± 0.13	1.11 ± 0.76
Yellow-rumped Warbler (*Dendroica coronata*)	2.89 ± 0.52	4.40 ± 0.61
Black-throated Gray Warbler (*Dendroica nigrescens*)	0.51 ± 0.39	0.07 ± 0.09
Hermit Warbler (*Dendroica occidentalis*)	2.67 ± 0.92	4.42 ± 0.65
Western Tanager (*Piranga ludoviciana*)	3.96 ± 1.01	4.16 ± 0.54
Purple Finch (*Carpodacus purpureus*)	0.09 ± 0.18	0.04 ± 0.05
Evening Grosbeak (*Coccothraustes vespertinus*)	0.04 ± 0.09	0.22 ± 0.23
Pooled	12.13 ± 2.16	18.49 ± 1.71
Cavity-nesting species		
Northern Flicker (*Colaptes auratus*)	0.24 ± 0.15	0.60 ± 0.21
White-headed Woodpecker (*Picoides albolarvatus*)	0.15 ± 0.15	0.53 ± 0.18
Red-breasted Sapsucker (*Sphyrapicus ruber*)	0.07 ± 0.09	0.31 ± 0.26
Hairy Woodpecker (*Picoides villosus*)	0.20 ± 0.19	0.45 ± 0.24
Pileated Woodpecker (*Dryocopus pileatus*)	0.13 ± 0.13	0.02 ± 0.04
Mountain Chickadee (*Poecile gambeli*)	1.47 ± 0.83	2.89 ± 0.52
Red-breasted Nuthatch (*Sitta canadensis*)	1.51 ± 0.33	2.00 ± 0.16
Brown Creeper (*Certhia americana*)	0.93 ± 0.63	1.38 ± 0.96
Pooled	4.70 ± 1.52	8.18 ± 1.01
All nesting species pooled	31.00 ± 2.38	48.55 ± 4.34

TABLE 3. Number of nests of each species found on unthinned and thinned plots (followed by number of nests with known fates in parentheses), and number of successful nests observed on unthinned and thinned plots. Species with significantly more nests found on the thinned plots than on the unthinned plots are indicated in bold type; no species' nests were found significantly more often on the unthinned plots. Data are from northern California, 1998–2000.

	Unthinned plots		Thinned plots	
	All nests	Successful nests (%)	All nests	Successful nests (%)
Ground-nesting species				
Mountain Quail	0 (0)	0 (0.0)	2 (2)	0 (0.0)
Townsend's Solitaire	4 (4)	2 (50.0)	7 (7)	3 (42.9)
Nashville Warbler	2 (2)	2 (100)	0 (0)	—
Spotted Towhee	6 (6)	3 (50.0)	7 (7)	3 (42.9)
Dark-eyed Junco	**22 (22)**	**10 (45.5)**	**51 (50)**	**23 (46.0)**
Fox Sparrow	0 (0)	0 (0.0)	7 (7)	2 (28.6)
Shrub-nesting species				
Dusky Flycatcher	**0 (0)**	—	**76 (67)**	**23 (34.3)**
Hermit Thrush	1 (1)	0 (0.0)	4 (4)	2 (50.0)
Cassin's Vireo	10 (8)	3 (37.5)	22 (21)	9 (42.9)
Yellow Warbler	0 (0)	—	6 (6)	4 (66.7)
MacGillivray's Warbler	0 (0)	—	2 (2)	2 (100)
Black-headed Grosbeak	1 (1)	0 (0)	16 (16)	9 (56.3)
Lazuli Bunting	10 (10)	6 (60.0)	6 (6)	4 (66.7)
Chipping Sparrow	0 (0)	—	10 (6)	5 (83.3)
Canopy-nesting species				
Sharp-shinned Hawk	1 (0)	0 (0.0)	0 (0)	—
Northern Goshawk	1 (1)	0 (0.0)	0 (0)	—
Anna's Hummingbird	1 (1)	0 (0.0)	2 (2)	1 (50.0)
Calliope Hummingbird	2 (2)	2 (100)	0 (0)	—
Western Wood-pewee	0 (0)	—	1 (1)	1 (100)
Hammond's Flycatcher	**1 (0)**	**0 (0.0)**	**19 (16)**	**10 (62.5)**
Steller's Jay	3 (2)	1 (50.0)	0 (0)	—
American Robin	6 (5)	2 (40.0)	5 (5)	0 (0.0)
Warbling Vireo	**1 (1)**	**1 (100)**	**22 (19)**	**6 (31.6)**
Yellow-rumped Warbler	8 (7)	2 (28.6)	17 (13)	9 (69.2)
Black-throated Gray Warbler	4 (2)	1 (50.0)	0 (0)	—
Hermit Warbler	4 (3)	2 (66.7)	6 (4)	2 (50.0)
Western Tanager	20 (18)	5 (27.8)	21 (18)	5 (27.8)
Purple Finch	1 (0)	0 (0.0)	0 (0)	—
Evening Grosbeak	0 (0)	—	1 (1)	0 (0.0)
Cavity-nesting species				
Northern Flicker	4 (4)	3 (75.0)	12 (9)	3 (33.3)
White-headed Woodpecker	**2 (2)**	**2 (100)**	**12 (11)**	**7 (63.6)**
Red-breasted Sapsucker	**0 (0)**	—	**11 (9)**	**7 (77.8)**
Hairy Woodpecker	1 (1)	0 (0.0)	4 (4)	3 (75.0)
Pileated Woodpecker	1 (1)	1 (100)	0 (0)	—
Mountain Chickadee	**4 (3)**	**1 (33.3)**	**19 (14)**	**6 (42.9)**
Red-breasted Nuthatch	**8 (5)**	**3 (60.0)**	**21 (16)**	**11 (68.8)**
Brown Creeper	10 (9)	7 (77.8)	9 (6)	3 (50.0)
All Species	**139 (121)**	**59 (48.8)**	**398 (349)**	**163 (46.7)**

the visual detectability of birds, particularly those near the observer (i.e., within 50 m). Therefore, the true differences in bird abundances between the two sets of plots may be even greater than we report.

Except for shrub-nesting species, avian community composition was similar for thinned and unthinned plots, but over 1.5 times as many birds were detected on the thinned plots. Nest-finding and point count
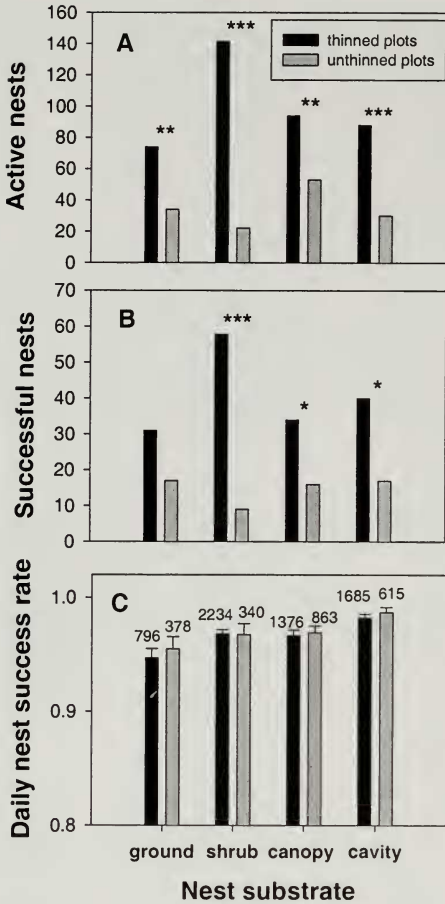
FIG. 1. We observed many more (a) active nests and (b) successful nests on thinned plots than on unthinned plots. Daily nest success rates (c) of thinned and unthinned plots were indistinguishable. Numbers above error bars indicate the number of observation days on which each success rate is based. * indicates $P < 0.05$, ** indicates $P < 0.001$, and *** indicates $P < 0.0001$.

data both corroborate that shrub, canopy, and cavity-nesting species occurred on the thinned plots at much higher densities than on the unthinned plots. Results for ground-nesting species were slightly more ambiguous. Point count data suggest that ground-nesting species were equally abundant on thinned and unthinned plots, but we found significantly more ground nests on the thinned plots than on the unthinned plots. Of course, nest-searching results must be interpreted with some caution, as they also could be biased by differences in detectability between the thinned and unthin-

ned plots. Still, it seems very unlikely that any such differences could have been of high enough magnitude to explain our finding nearly three times as many nests (all species pooled) on the thinned plots (Table 3).

The difference in bird communities between the thinned and unthinned plots was most extreme among shrub-nesting species. Dusky Flycatchers, the single most commonly detected species on the thinned plots (mean of 29.89 detections per point count transect; 76 nests found), were virtually absent from the unthinned plots (mean of 0.33 detections per point count transect; no nests found). Except for Black-headed Grosbeak and Lazuli Bunting (*Passerina amoena*), we detected each of the nine shrub-nesting species we found nesting on one or more of the study plots at least twice as often on the thinned plots as on the unthinned plots.

The thinning protocol was implemented between 1990 and 1993, 5–8 years before the beginning of our study, and 8–11 years before the end. Although we did not quantify shrub cover before the forest was thinned, comparison with the unthinned plots suggests that thinning successfully stimulated vigorous shrub growth, which was then associated with elevated densities of birds. While this makes intuitive sense for shrub-nesting species, it is less clear why canopy and cavity-nesting species would be more abundant on thinned plots with substantially greater shrub cover. For birds with life histories less tied to shrubs, extent of the shrub layer may be a proxy for other ecological variables with which it correlates, rather than a direct causal factor. Hammond's Flycatchers, for example, forage on flying insects by sallying into the open spaces beneath the overstory canopy and between trees (Mannan 1984, Hagar et al. 1996). This species may therefore be responding to the increased space available for foraging underneath the canopy, rather than the increase in the extent of shrubs, although increased shrub growth likely results from the same conditions that produce good Hammond's Flycatcher foraging habitat.

Even species such as Golden-crowned Kinglets (*Regulus satrapa*) and Brown Creepers (*Certhia americana*), which usually are associated with mature, shaded forest stands (Ziener et al. 1990) did not appear to be substan-

tially negatively impacted by the thinning. Both species were relatively common on thinned as well as unthinned plots, with statistically indistinguishable numbers of detections in the two plot types. We were unable to locate any kinglet nests, but found virtually identical numbers of Brown Creeper nests on thinned plots (9 nests) and unthinned plots (10 nests).

While nesting density differed substantially between the two sets of plots, nest success rates did not. Although pooling nest success data by nesting group could potentially mask poor nesting success of particular species (Mannan et al. 1984), generating adequate sample sizes for studying nest success rates of more than a few species is notoriously difficult. Reliable estimates of species specific nest success rate generally require at least 20 nests (Hensler and Nichols 1981), and in many cases even 20 nests are far from adequate for detecting differences in nest survivorship between two groups (Nur et al. 1999). Where such large single species sample sizes are unavailable, pooling species by nesting group or other shared characteristics can provide an important function. Alarmingly low nest success rates of groups of species with similar nesting habits or other shared characteristics can signal researchers to target the constituent species for more intensive study, of the sort that might generate the large sample sizes needed for species specific estimates.

Brown-headed Cowbirds (*Molothrus ater*) were detected in low numbers on the thinned plots, and virtually never on the unthinned plots. During the three years of this study, we confirmed cowbird parasitism at six nests, including three Cassin's Vireo (*Vireo cassinii*) nests, two Warbling Vireo (*Vireo gilvus*) nests, and one Yellow-rumped Warbler (*Dendroica coronata*) nest. While such a small sample size prevents any firm conclusions, all six parasitized nests were located on the thinned plots, raising the possibility that forest openings created by the thinning protocol may have made nesting songbirds more vulnerable to cowbird parasitism.

Overall, nests on unthinned plots exhibited slightly higher success rates than nests on thinned plots, but the differences were not significant. Even if real, the differences were not large enough to compensate for the compar-

atively low density of shrub, canopy, and cavity nesters on unthinned plots; the thinned plots clearly produced more fledglings than did the unthinned plots.

The fact that our results come from just two clusters of study plots on adjacent slopes limits our ability to extrapolate our findings to other parts of the Sierra Nevada, or to pin down a definitive causal relationship between silviculture treatments and avian community composition. Nevertheless, our results suggest that forest conditions which stimulate vigorous shrub growth, particularly growth of deer brush, may be highly beneficial to the majority of breeding birds in the Sierran mixed conifer community, even if the precise ecological mechanisms for canopy- or cavity-nesting species remain obscure. Multispecies management is usually a balancing act among the conflicting needs of different species of concern. The combination of commercial and biomass thinning on our study plots appears to have provided a rare exception to the general rule that habitat attributes benefiting some species of concern are detrimental to others. Even birds normally thought of as forest interior species, such as Brown Creepers and Golden-crowned Kinglets, did not appear to be deleteriously affected by the thinning, while many species may have benefited. If our results hold true across the larger Sierran landscape, then thinning that promotes the growth of deer brush and other shrubs in Sierran mixed conifer stands affected by historical fire suppression may be a useful tool for enhancing habitat value for forest-nesting birds, at least during the breeding season. We stress, however, that these results do not necessarily imply that forest thinning will increase nesting bird density in stands that have experienced more natural fire regimes. Rather, our results suggest that thinning practices that spur shrub growth may be valuable for enhancing the habitat value of forest stands comprising densely packed, stunted conifers, and very few shrubs.

Finally, detectability estimation methods such as distance sampling (Buckland et al. 2001), the double-observer approach (Nichols et al. 2000), or double sampling (Bart and Earnst 2002) should be incorporated into study designs whenever feasible. Our comparison of the ratios of the number of detec-

tions <50 m and >50 m from the observer may be a useful technique for researchers interested in determining the potential value of data sets based on limited radius point counts but with no adjustments for detectability.

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